The nesting of *Pareumenes brevirostratus* (Saussure), involving a primitive form of co-operation

BY

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Pareumenes brevirostratus is a squatter species practising mass provision. ing. The only individual watched provisioned with pyralid prey, and all her offspring entered diapause, one for two seasons. While working she was disturbed by individuals of *Rhynchium brunneum* and *R. carnaticum*. Some of the mutual reactions of these wasps may simulate the early stages of social behaviour in some hymenoptera.

INTRODUCTION

We know no description of the breeding biology of any[3] member of the genus *Pareumenes* Saussure, certainly none for the present species, for which van der Vecht (1963, p. 19) gives the bibliography, and a reappraisal.

We are presenting the one diary which we have collected. This must be exceptional for the species considered but reveals capabilities of the solitary vespoids which suggest speculation on the origin of social behaviour.

Members of the 4 vespoid families referred to have been identified by Dr. J. van der Vecht of Leiden, Dr. K. Iwata of Sasayama has examined the lepidopteran larvae used as prey, and Dr. M. Chujo of Takamatsu has identified the parasitic beetle. We are extremely grateful to these authorities for their help.

THE NEST BOXES

Nest boxes were narrow strips of wood each numbered by an arabic figure hung up on walls and vertical fitments of our house in Bhubaneswar. In these had been bored a single row of short horizontal blind tunnels

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[3] *Pseumenes depressus* (Saussure) whose habits are described by Iwata (1964) who also refers to the previous literature, has in some of this, been regarded as a species of *Pareumenes* (van der Vecht 1963, p. 21).

numbered in roman figures from top to bottom. The circumference of one tunnel was about 1·75 cm. distant from those adjacent to it. In any one strip all the tunnels were one length but of two diameters. As they were bored with tools calibrated to 1/16″ (1·6 mm.) this is the unit used in Table 1 which gives the diameters of the tunnels, their horizontal lengths and the locations of the three nest boxes referred to in this paper. A tunnel is referred to by the two numbers given above e.g. 7.XV and the wasp cell built in it is referred to by the same double number preceded by the initials of its mother's taxonomic name and her serial number.

TABLE 1

1.	diameter	6.	diameter	7.	diameter
I	3	I	4	I	4
II	4	II	4	II	7
III	3	III	5	III	4
IV	4	IV	4	IV	7
V	3	V	5	V	7
VI	4	VI	4	VI	4
VII	3	VII	5	VII	7
VIII	4	VIII	4	VIII	4
IX	3	IX	5	IX	7
X	4	X	5	X	4
		XI	5	XI	7
		XII	4	XII	7
		XIII	4	XIII	7
		XIV	4	XIV	7
		XV	5	XV	4
		XVI	5	XVI	4
				XVII	4
length of tunnels	12		16		24
location	indoors		on verandah facing 12° W of S		on verandah facing 12° W of S

all measurements in 1/16″ or 1·6 mm.

THE BEHAVIOUR OF ONE FEMALE ; *P.b.*1

On 12/9/1964, first noticed at 10.45, a long petiolate russet and yellow vespoid later identified by her offspring as a member of *Pareumenes brevirostratus* (Saussure), surprised us by working for 12 minutes cleaning two of the empty cells of the giant nest of *Eumenes emarginatus conoideus* (Gmelin) *E.e.c.* 10, on which we have previously published (Jayakar & Spurway 1965). We were unaware that wasps of this body form, which is sometimes described as an adaptation to oviposition in a small mouthed pot, could have squatter habits. Next day (13/9) a similar wasp (now, knowing the rarity of the species, presumed to be the same individual) was seen in the same area.

No wasp of this species was seen again until 18/9 when in the morning one (she ?) was seen flying round electric wiring fitments indoors, and at 15.12 she was seen feeling inside tunnel 1.VI. When she left it was found that at the blind end of this tunnel there was suspended a eumenid egg of about the size laid by some species of *Rhynchium* Spinola. No individual belonging to *Rhynchium* has used any tunnels in this nest box before or since. This is interpreted as being because they are too small. At the time described, nest box 1 was empty and no other wasp used it before she deserted it.

She did not pernoctate (Jayakar & Spurway 1966) in this tunnel but on 19/9 was seen feeling tunnels 1.VI, 1.II and 1.IV as early as 07·32. She provisioned tunnel 1.II and had sealed it by 09·45 ; at 09·54 she had returned to seal 1.VI and at 10.02 she was again working on 1.II. 1.II must have contained an egg with adequate provisions because the individual by which the species has subsequently been identified, emerged from it. At 11.39 the wasp was captured etherised and a spot of yellow enamel paint was applied to the thorax. From this time therefore the identity of *P.b.*1 was established.

1.VI was subsequently reopened by an *Antodynerus flavescens* (Fabricius), *A.f.* 32 on 26/9/1964. As this female had simultaneously opened a cell in 1.I which she herself had provisioned and sealed on 24/9 we do not know from which came the many prey dropped on the floor.

On 20/9, *P.b.*1 once more investigated nest box 1, and 2 hours later had returned to the verandah and the large deserted nest of *E.e.c.*10.

She was not seen again for 13 days when on 3/10 she was found, still painted, investigating nest box 7 on the same verandah and on a similar window shutter to *E.e.c.*10. An egg was seen in 7.VII.

On 4/10 this egg was absent. *P.b.*1 returned and worked on 7.VII for over two hours, occasionally investigating and entering 6.III a few metres away and in a similar position. During this time it was established both that she spent much time in the tunnel facing out as do the inconspicuously petiolate squatters of the genera *Rhynchium* and *Antodynerus* Saussure, and *Subancistrocerus sichelii* (Saussure), and also if the tunnel has a sufficiently large diameter she could, like these, enter it head first and turn round inside. As with the other squatters the egg was laid suspended during one of these periods and first seen again in 7.VII at 10.07. This egg was provisioned with a species of green glassy caterpillar which becomes yellowish when preserved in alcohol. By 17.16 this cell was sealed, the lid being 10 mm. within the tunnel, and its contents were thus called *P.b.*1, 7.VII.1. It was hoped that another egg 7.VII.2 would be laid and provisioned distal to this diaphragm. *P.b.*1 did not pernoctate where we could observe her.

During 4/10 a *Rhynchium brunneum* (Fabricius) *R.b.*4 had begun working on nest box 7, sealing 7.XIV with 2 separate diaphragms, after

which she too was marked ; she sealed 7.IV (details of sealing unknown), and oviposited and provided two prey in 7.II, but did not pernoctate in it. This is exceptional for individuals of this species of *Rhynchium*.

It was noticed that *R.b.*4 was provisioning with the same species of prey as *P.b.*1. This has been confirmed by Professor Iwata who informs us that this is a species of pyralid moth, but because the early stages of so many Indian lepidoptera are undescribed, he is unable to classify it further.

On 5/10, *R.b.*4 continued provisioning 7.II and sealed it just before 9 o'clock. Though the tunnel only contained one offspring she made two discrete lids with a space of over 1 mm. between them. The second lid, often made by these *Rhynchium* are more granular than the first, and these granulations are usually spread in ribbons around the mouths of the tunnels over the wooden surface of the nest box. In texture, as in timing, these second lids are convincingly comparable with the crépissage of the pot building *Eumenes* Latreille (Jayakar & Spurway 1965). At 09.28, *R.b.*4 felt 7.IV and entered 7.V, but 5 minutes later she arrived with mud and after feeling 7.V and 7.VI she began making a diaphragm level with the surface over the mouth of 7.VII which *P.b.*1 had sealed 10 mm. within the tunnel the previous afternoon. Four minutes later, when *R.b.*4 was next seen to arrive with mud, *P.b.*1 was present on 7.VII ; *R.b.*4 walked up to 7.V but immediately returned to 7.VII and *P.b.*1 made way for her. *R.b.*4 began working the mud into the incomplete diaphragm over 7.VII ; *P.b.*1 attacked her. Both wasps pecked at each other with their mandibles and both flew away at 09.38. We did not see *P.b.*1 again on 5/10, but *R.b.*4 finished the second lid on 7.VII and put on the crépissage ribbons. She immediately began working in tunnel 7.IX at 10.10 arriving with mud which she put in 7.IX and then turned round in the tunnel into the ovipositional position. At 10.22 she was again seen in 7.IX and at 10.46 she was absent and an egg was present in 7.IX. The deposit behind this egg at the bottom of the tunnel was unexpectedly white. These times are given in detail because they led us to believe that the egg in 7.IX had been laid by *R.b.*4. Very few eggs in our records of all species except those of females watched continuously, are associated with their putative mothers by a closer sequence of observations. However, though this egg did not produce an imago we became subsequently convinced that the larva recovered from this cell had come from an egg laid by *P.b.*1. *R.b.*4 was not seen again on 5/10 but one pyralid larva was found added to 7.IX by 13.40, but no more during the afternoon.

On 6/10 by 07.53, 2 larvae were present in 7.IX, at 08.08 *P.b.*1 was seen inserting a larva, and 2 more were added before 09.17. At this time *R.b.*4 arrived also carrying a similar larva, landed on 7.IX and immediately threw her larva away so that it fell from her at an angle.

*R.b.*4 then removed the 5 larvae in tunnel 7.IX flying with each in turn to drop it several metres from the nest box. The egg alone was left in 7.IX, again, and incorrectly, confirming the previous diagnosis that it had been laid by *R.b.*4. At 10.29 *P.b.*1 began reinserting fresh larvae into 7.IX, and 3 were again found on the verandah at 12.52, the egg being once more left alone.

At 13.44 there was once more a larva in 7.IX and at 13.46 *P.b.*1 brought mud, went to nest box 6, flew to 7, and found 7.IX, but after entering it returned to the garden still carrying the mud with her. It was now noticed that the egg had hatched and the larva was hanging from the shell so that it touched the prey on the floor of the relatively enormous tunnel. Between 14.00 and 14.16 *P.b.*1 was seen bringing 3 loads of mud, with the last she remained inside until 14.23, working on a diaphragm deep in the tunnel.

Meanwhile, at 14.18, *R.b.*4 arrived with a larva. After hovering near 7.IX she left with the larva and returned 3 minutes later without a load. She then walked all over nest box 7 entering and feeling 7.XII and 7.XIII but always pausing near 7.IX. She was hovering when *P.b.*1 came out and stood over 7.IX before flying for a moment to return and feel the rim of 7.IX. When *P.b.*1 left we saw that the diaphragm within 7.IX was newly completed. The next load of mud was brought at 14.29. *This was brought by R.b.*4 *who added it to the diaphragm made by P.b.*1.

*R.b.*4 brought 6 more loads of mud during the afternoon, and though with the first she entered 7.IX, she put it down on 7.XIV, with the second she again flew to 7.IX, but only hovered over it, and continued adding to the crépissage of 7.XIV. During this work she was continually feeling other tunnels, the typical behaviour when a cell has been completed and a new tunnel is being selected. She laid in 7.XIII and returned through heavy rain to typically pernoctate in it. *P.b.*1 meanwhile brought a load of mud *and after feeling her previous diaphragm to which R.b.*4 *had contributed, began with this load a second diaphragm at the mouth of the tunnel.* To this she added 4 more loads during the afternoon. During this she was several times attacked by a *Rhynchium carnaticum* (Fabricius), *R.c.*5, who at 15.14 had begun investigation of 7.V.

Thus on 6/10 both *P.b.*1 and *R.b.*4 worked mud in tunnel 7.IX, and though *P.b.*1 alone was seen inserting prey, no other cell was open to receive the larvae brought by *R.b.*4 at 09.17 and 14.18, and it is difficult not to assume that they too were intended for 7.IX.

On 7/10, *R.b.*4 continued work on 7.XIII, *R.c.*5 on 7.V, and *P.b.*1 after feeling the lid of 7.IX spent many hours examining tunnels 7.XII and 7.XI. *P.b.*1 and *R.b.*4 buzzed round one another many times stimulating each other to cease work and fly. *R.b.*4 sealed 7.XIII and began

examining 7.XII and 7.XI herself. This produced much more definite aggressive behaviour, especially by *R.b.*4. *R.b.*4 for some time left the nest box to examine a piece of bamboo. Between 13.25 and 13.27, an exceptionally short interval, *P.b.*1 laid an egg in 7.XI and brought the first prey for it at 13.37. *R.b.*4 at 14.00 was in 7.XII facing out i.e. she might be assumed to be ovipositing. She was disturbed by an *Antodynerus flavescens* on the surface of the nest box. She walked out of tunnel 7.XII and very slowly, while feeling the surface of the nest box, walked up to 7.XI, removed and dropped the prey from 7.XI, and returned to 7.XII. This she did not re-enter backwards until after much feeling of the tunnel with her antennae and hovering over it. *R.b.*4 laid an egg in 7.XII the same evening and pernoctated in it. At 15.00, *P.b.*1 arrived at 7.XI without a load, worked in it, and then turned round inside it so she was facing out. She then repeated the curious wriggling which had been noticed before when she was ovipositing, or had just oviposited. After 53 minutes she walked out, and only 1 egg was seen in tunnel 7.XI.

On 8/10 both *P.b.*1 and *R.b.*4 continued provisioning though *R.b.*4 changed her prey. At 11.47 immediately after sealing 7.XII, *R.b.*4 removed 7 larvae from 7.XI and for the first time the egg as well. She then removed the egg laid by *R.c.*5 in 7.V. *R.c.*5 immediately laid a new egg, provisioned and sealed it, and laid another egg in the same tunnel. Curiously this outer egg, *R.c.*5, 7.V.2 metamorphosed successfully, whereas the inner egg was parasitized by the rhipiphorid beetle *Macrosiagon ferrugineum* (Fabricius). *R.b.*4 then inspected nest box 6 but finally transferred her attentions to the nest *E.e.c.*10 in which she laid 10 eggs.

*P.b.*1 after examining 7.XI moved to the lid of 7.XII sealed by *R.b.*4 10 minutes previously, from this she took wet mud, and immediately began a diaphragm 8 mm. deep in the now completely empty 7.XI. She continued working on this lid 7.XI, fetching mud from the garden for the next 1¾ hours. She then disappeared for good. During the 6 days, 3-8/10, 2 individuals of *Antodynerus flavescens* were also working in nest box 7, all 17 tunnels of which were sealed by the evening of 8/10.

The offspring

We assume we had three offspring of *P.b.*1, namely 1.II, 7.IX and 7.VII ; all entered diapause, and were removed from the tunnels to corked glass tubes. 1.II, a ♂, pupated on 7/7/65 emerged on 20/7 from the pupa and was killed on 22/7 when he had become active. 7.IX was judged to have died on 23/7/65, but 7.VII did not die until just before 17/5/66. We have had only one other larva remain in diapause for 2 seasons, and this interestingly, but perhaps not significantly, was from the second egg laid in 1.I by *A.f.*32 on 27/9/64 after she had removed both an egg and pro-

visions of her own from this tunnel, and that laid by *P.b.*1 in 1.VI. This female later squatted in *E.e.c.*10 also.

That these larvae diapaused confirms that 7.IX was the offspring of *P.b.*1 and not *R.b.*4. Five of the offspring of *R.b.*4 already described developed to imagines, and 8 laid by her in *E.e.c.* 10. These 13 all emerged the same autumn, the longest preimaginal period being 29 days. Therefore the larva in 7.IX would not only have been the only member of the family to diapause, but would have had both older and younger sibs that did not.

Discussion

Despite the bizarreness of this single history, there can be little doubt that despite its body shape *Pareumenes brevirostratus* is a typical squatter practising mass provisioning. It also competes with the sibling species *Rhynchium brunneum* and *R. carnaticum* for nest sites, and with the former at least for prey. We have not yet recognised the ecological differences which, according to Gause's principle (*see* e.g. Lack 1966), must be expected between these two morphologically similar species of *Rhynchium*. In a so-called domestic, environment, this individual of *P. brevirostratus* was a slower worker than the individual of *R. brunneum* with which she competed, but wasps vary much, even the same individual at different periods of their lives, in their speed of work (Jayakar & Spurway 1965). Also, in this history, though the *brunneum* destroyed more of the effort of the *brevirostratus* than vice versa, more of the effort of the *brunneum* effectively contributed to the care of the *brevirostratus* offspring than vice versa.

The repeated removal of prey brought by the *brevirostratus* by the *brunneum* was not a simple example of the extreme sensitivity of solitary vespoids to alien handling of their prey (Roubaud 1916), for this prey was removed by the *brunneum* from the *brevirostratus* eggs. This probably was because the prey brought by the *brevirostratus* was of the same species as that which *brunneum* was, at that time, collecting, probably for the same egg. If the prey had been of a different species she might not have been disturbed by the alien wasp smell on it because she would not have interpreted this as interference with her own work.

Most important is that though such wasps resent so strongly an alien smell on prey, they have no such reaction to an alien smell on mud, though the gastric secretion with which this mud is mixed would be expected to be vivid, especially before it had dried.

One of the suggestions for an origin of the co-operation shown by the social hymenoptera is that they might be descended from species whose solitary nests were constructed in aggregates. They might sometimes have worked on each other's constructs because these incomplete con-

structs, independently of the builder, provided the releasers to evoke the relevant behaviour. We have previously described (1963) how the sphecoid *Chalybion bengalense* (Dahlbom) is stimulated to deposit her faecal crépissage on the naked mud lids of *Antodynerus flavescens*. The present history records how similar effective co-operation may be stimulated while the work is in progress. This co-operation was not only performed by one animal, but *accepted* by the other, in a context where much mutual destruction of work also occurred, and where all reactions by the 2 wasps to each other, face to face, were aggressive.

As may have been implicit already, during the period considered these nest boxes provided baits, producing an artificial concentration of individual wasps in an environment in which the boxes themselves provided a somewhat unnatural, or experimental, feature.

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